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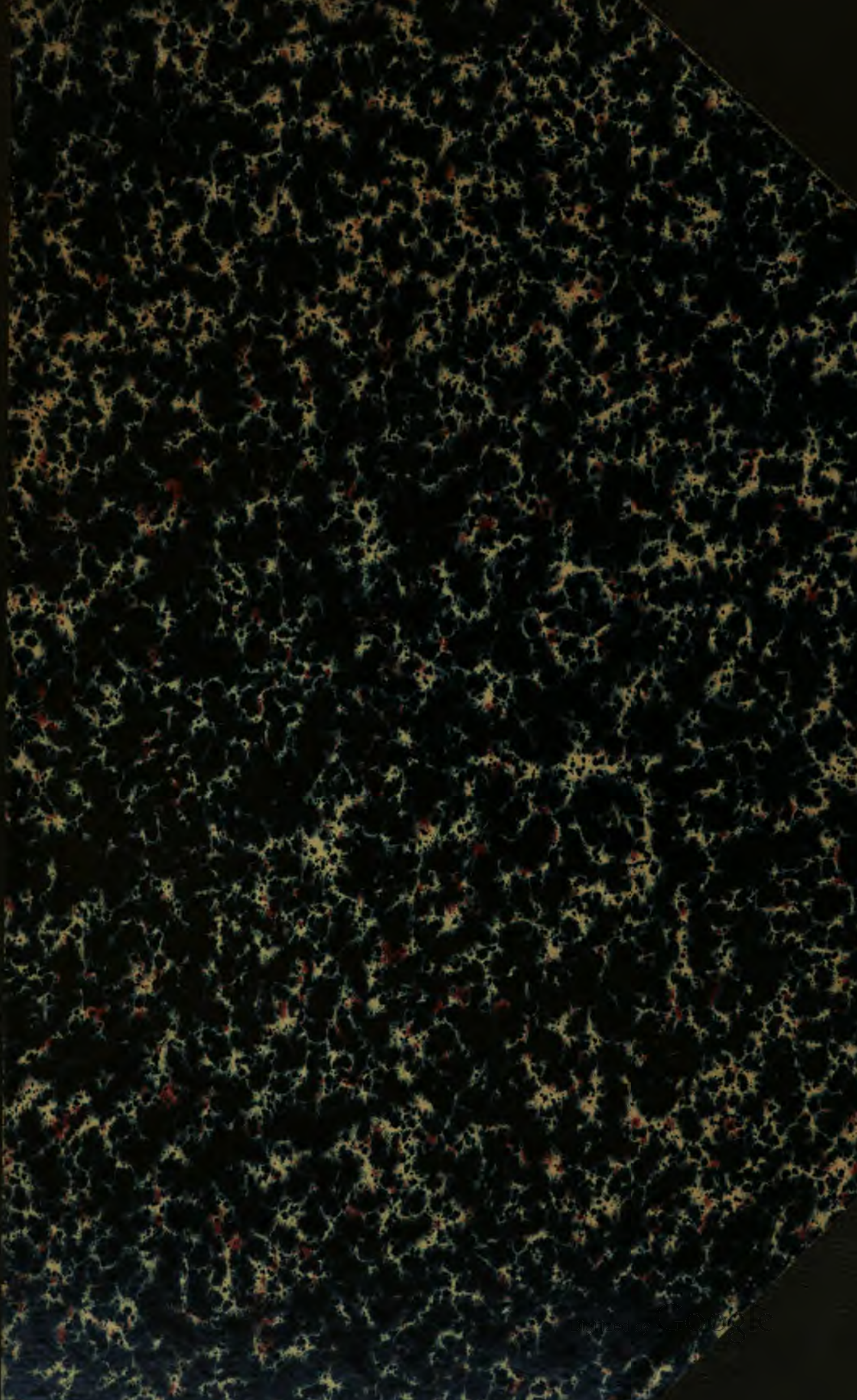

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W. G. FARLOW.

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THE DEVELOPMENT OF THE OSTRICH FERN,

BY DOUGLAS HOUGHTON CAMPBELL, Ph.D.

W. G. FARLOW.

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II. THE DEVELOPMENT OF THE OSTRICH FERN, ONOCLEA STRUTHIOPTERIS.

By DOUGLAS HOUGHTON CAMPBELL, Ph.D.

(Walker Prize Essay, 1886)

AMONG the most characteristic ferns of the northern United States are those belonging to the genus Onoclea, represented by three species, two of which, *O. sensibilis*, L., and *O. struthiopteris*, Hoffm., are found throughout the northeastern United States, the latter species, the subject of this memoir, being less generally distributed, though locally abundant. It also occurs throughout northern Europe and Asia.

The sporangia in this fern are borne in great numbers on the back of the fertile fronds, and as these remain standing through the winter after the sterile fronds have decayed, spores can be obtained at all seasons of the year. These retain their vitality for several months after being gathered, so that when the plants are common, abundance of material is constantly on hand. This fact, together with the ease with which the spores can be germinated, makes the plant a specially valuable one for study.

The observations here recorded were begun in the spring of 1882, and were continued, with more or less interruption, through the autumn of 1885. The points of most importance discussed are the following:

The presence of a third coat in the spore.

The marked dioecism displayed by the prothallia.

Formation and development of the apical cell of the prothallium.

Continuity of the protoplasm in the cells of the prothallium.

Development of the antheridium and antherozoids.

Absence of the ventral canal-cell in the archegonium.

Succession of the divisions of the embryo and the establishment of the apical cells of its different members.

Development of the different tissues of the embryo.

Development of the leaf from the apical cell, and the relation of the different tissues of the leaf to the segments of the apical cell.

Method of formation of the pinnae.

Development of the stem from the apical cell.

Development of the sporangium.

Section I. Prothallium.

The spores are of the so-called bilateral form, oval in shape and protected by a firm, dark brown outer coat, the exospore, which is provided with ridges or folds, usually arranged so as to enclose an irregularly polygonal area, other ridges running from the angles. The spore is slightly flattened on the side originally in contact with its fellow, in the mother-cell, and the exospore on this side is smooth. Besides the exospore there are two other coats: a middle one that does not appear to have been previously noted in ferns, and the endospore. The middle coat is not readily seen before germination, but that it is not unmodified cellulose is shown by the fact that the prolonged action of sulphuric acid and iodine does not color it blue. It is plainly seen in cases where the opaque exospore has become detached before germination, as it must be ruptured before the endospore can protrude. The exospore seems to be only slightly attached, readily separating on slight friction, and is often thrown off by the swelling of the spore on the absorption of water.

On examining dry spores after the removal of the exospore, they are found to be flattened on one side, but in a few minutes after being placed in water, by its absorption they become distended and all trace of flattening disappears, the spore then being almost perfectly oval in form (Pl. 4, fig. 1). They contain abundant chlorophyll which is sometimes nearly uniformly distributed throughout, but is commonly more abundant in the center. Besides the chlorophyll, the protoplasm contains other granules, not, however, of starch. Oil is often to be detected in drops of considerable size but is usually uniformly distributed. At the center of the spore, but usually nearly concealed by its dense contents, is a small, but sharply defined nucleus.

Under favorable circumstances, the spores begin to germinate in from three to five days. The early stages can best be observed by simply growing the spores in water, and keeping them in a warm place in a moderately strong light; but perfect prothallia cannot be thus obtained.

The first sign of germination, in cases where the exospore has been thrown off, is a splitting of the second, or middle coat, for nearly the whole length of the spore, and through the fissure thus formed the endospore protrudes (Pl. 4, figs. 2, 3). Usually one end of the spore at this time is more transparent than the rest, being wholly, or in part, destitute of chlorophyll. This transparent end becomes shut off from the body of the spore by a septum nearly at right-angles to the longer axis of the spore, and becomes the first root-hair (Pl. 4, figs. 2–4, 6). This elongates rapidly, attaining in the course of two or three days four or five times the length of the original spore. The body of the spore has also elongated by this time to more than twice its original size, and becomes further divided by a septum nearly parallel to the first. The terminal cell continues to increase in length, and new septa parallel to the first are formed thus causing the prothallium to assume the filamentous or protonemal stage (Pl. 4, figs. 4, 6). By the end of the first week many of the prothallia show divisions at right angles to those first formed, this sometimes occurring in the second or third cell, but not usually until a row of three or four cells has been formed. About the same time a second root-hair is formed from the basal cell. A small papilla is formed on one side which is cut off from the cell by a septum, and rapidly elongating assumes the form of the first (Pl. 4, fig. 5 r'). Like this it contains little or no chlorophyll. As growth progresses the chlorophyll granules, which had at first been crowded together, become more separate and very distinct. The protoplasmic layer in which the chlorophyll granules are embedded lines the walls of the cells, the center of the cell being occupied by a large sap-cavity. The nucleus, which is sharply defined, and usually contains an evident nucleolus, is round in outline, and lies close to the wall of the cell. In the root-hairs the protoplasm, near the growing end, is finely granular, and a few larger granules are scattered through the peripheral protoplasm. In the young hairs, some of these are faintly colored with chlorophyll but this seems to be finally lost.

If the protoplasm of the cells of the prothallium is contracted, *e. g.*, by a solution of sodium chloride, and then stained, the continuity of the protoplasm can be easily demonstrated. Delicate threads of protoplasm can then be detected connecting the protoplasmic masses of adjacent cells, apparently passing through small openings in the wall.

By the end of the second week the flattened form of the older prothallia begins to be marked, on account of the division of the cells in two planes, and about a week later the larger ones show the beginning of the sinus in the front margin, causing it finally to assume the heart-shape usually met with in the larger prothallia of ferns. This form is usually quite pronounced by the end of the first month (Pl. 4, fig. 13). It is brought about in the following way: after a row of several cells has been formed, the terminal cell becomes divided by a wall nearly at right angles to the earlier ones. In the cells thus formed, transverse walls are formed which, however, generally diverge somewhat from an exact right angle with the median wall, being turned slightly forward, thus forming two cells that are nearly triangular in shape. One of these becomes the apical cell of the prothallium, the other behaving like the ordinary cells. The apical cell becomes next divided by a wall parallel to one of its lateral walls, and next by a similar one parallel to the other side. This process is repeated, resulting in two series of segments lying alternately right and left, thus rapidly increasing the breadth of the apex of the prothallium (Pl. 4, figs. 7–11). Occasionally, two segments appear to be cut off from the side in succession, but this is probably exceptional. The first division in each segment is transverse, and divides it into an inner and an outer cell. The succeeding divisions do not always follow the same order, but usually the next wall divides the outer cell into two equal parts, and is perpendicular to the first one. Following this, the inner cell is divided into two by a transverse wall. Beyond this point there is great irregularity. However, the longitudinal growth of the segment exceeds the lateral growth, so that the end of the segment is pushed out beyond the apical cell. This combined with the rapid division of the marginal cells of the segment results in the formation of a deep sinus or cleft, in the front of the prothallium, in the bottom of which lies the apical cell. Where this growth is excessive, the two lobes of the prothallium sometimes overlap. Sooner or later the apical cell ceases to form lateral segments, and becomes divided by a transverse wall into an inner and an outer cell, in the same way that the segments were first divided (Pl. 4, fig. 12). The outer cell divides into two equal cells by a wall at right angles to the first, and the apical cell thus becomes obliterated, acting from this time on like the other cells. In cases where the prothallium is branched, as frequently occurs in the male prothallia, a new apical cell, dividing in the same way as the original one, may be formed at the end of a branch. One case was observed where the prothallium was divided into two branches, each having a perfect apical cell, the whole looking very much as if these two cells had originated from a bipartition of the original apical cell.

Soon after the obliteration of the apical cell, or sometimes before, the cells in its vicinity, which hitherto have divided in two planes only, now divide also by walls parallel to the surface of the prothallium, thus giving rise to a mass of cells occupying the bottom of the cleft in its front. In cases where the prothallium continues to grow for a long time and this process begins early, a thickened mid-rib is formed, running for nearly its whole length.

The foregoing account applies only to the larger prothallia, which are, for the most part, female. Many exceptions occur in the male prothallia, and the younger prothallia that are exposed to unfavorable conditions. If the spores are germinated in water, the cells become much longer and more slender, sometimes attaining four or five times the normal length without dividing. On the other hand, prothallia grown under normal conditions are to be met with in which no protonema is formed, but the second cell of the prothallium dividing by a longitudinal wall, the flattened form is assumed almost from the beginning. Where the spores are sown thickly, the male prothallia sometimes do not pass beyond the protonemal stage, the row of cells being terminated by an antheridium, and these simple prothallia are sometimes destitute of any root-hair (Pl. 4, fig. 15). While many of the male have much the form of the female, differing simply in their smaller size, they are more commonly of very irregular shapes, especially if they have attained some size, often being much branched and lobed, reminding one strongly of those of certain species of Equisetum. In some irregular forms, either no definite apical cell is formed, or else it is early lost.

Under favorable circumstances the first antheridia are mature in from five to six weeks from the time the spores are sown, and the first archegonia about three weeks later. With care they can be kept alive for a comparatively long time. A quantity of prothallia raised from spores sown Aug. 31, 1884, were kept through the winter, growing but little for about two months, from the last of November. They were removed to a warm room in January and given abundant light and moisture. Growth was resumed and an abundance of antheridia and archegonia were produced. The greater part of the female prothallia produced young plants, but a few that were not fertilized were alive a full year from the time that the spores were sown. Most of the male prothallia had died a month or two previously. As the growth of the prothallium continues, new root-hairs are formed from the cells near its base; these arise sometimes from the margin, but more commonly from the lower surface of the cells; in exceptional cases from the upper surface.

Section II. The Sexual Organs.

The antheridia originate in the same way as the root-hairs. In the young prothallia they arise from the marginal cells; in the older ones, from the upper and lower surfaces as well. They begin as small prominences, usually close to the wall separating two adjacent cells. The protoplasm in the papilla is dense, especially in the middle, and contains small chlorophyll granules. A septum is then formed, by which the papilla, now the mother-cell of the antheridium, is shut off. This may be followed by a second wall parallel to the first so as to form a pedicel, but this is unusual (Pl. 4, fig. 29, P). Ordinarily, the first wall to be formed in the mother-cell is funnel-shaped, the base of the funnel being upward and the smaller end of the funnel in contact with the wall by which the mother-cell was first cut off (Pl. 4, fig. 16). Sometimes this wall is almost flat, or it may be convex downward but not reaching to the base of the antheridium. The second wall (Pl. 4, fig. 17) is nearly constant in form, dome-shaped or hemispherical and follows pretty closely the outline of the antheridium which has by this time grown rapidly and become nearly globular in shape. Finally, a third wall is formed in much the same way as the first, and like it subject to considerable variation (Pl. 4, fig. 18). The cell thus formed is the cap-cell and has its inner surface in contact with the upper part of the second wall. The antheridium now consists of four cells: an inner cell containing dense, finely granular protoplasm, but no chlorophyll; and three others which surround this, in which there is less protoplasm, but some small chlorophyll granules. Of the three outer cells the two lower are thus annular in form, except in cases where the first wall formed is not sufficiently convex to touch the basal wall of the antheridium, in which case the lower cell is discoid. About the time the cap-cell is formed, or sometimes before, the central cell begins to divide. The first wall (Pl. 4, fig. 20) is vertical, dividing the cell into nearly equal parts. This is followed by a second vertical wall (Pl. 4, fig. 23) at right angles to the first, so that when the antheridium is seen from above, the cells are arranged like quadrants of a circle. These undergo further divisions (Pl. 4, fig. 22) until there are about twenty cells. Their form is polyhedral, but the outer walls are rounded so that those on the outside of the mass appear almost globular. The protoplasm is highly refractive and finely granular and each cell is provided with a small but evident nucleus.

As soon as the sperm cells are fully grown the formation of the antherozoids begins. The protoplasm becomes somewhat more coarsely granular and the nucleus indistinct, though it does not actually disappear and can usually be demonstrated by staining. When it becomes more evident again, it is seen to have changed form and to have increased in size (Pl. 4, fig. 25). Instead of being globular, it is now crescent-shaped. It grows larger, becoming at the same time more curved (Pl. 4, fig. 26). This continues until it is soon evident that what was the nucleus of the cell is assuming the appearance of the complete antherozoid. Growth continues until the body of the antherozoid is in contact with the wall of the mother-cell, and lies coiled up within it, leaving, however, some remains of the protoplasm of the mother-cell lying between the coils. When the antherozoids are nearly mature, the walls of the sperm cells, which were hitherto in close connection, become partially absorbed leaving the separated sperm-cells free in the cavity of the antheridium. If an antheridium, in which the walls of the sperm-cells have undergone degradation, is placed in water, a very marked movement of the contents of the antheridium may sometimes be observed, due apparently to the absorption of water by the mucilaginous walls and their breaking down and dissolving through its action. Enough of the wall is left, however, to still enclose the antherozoid. By the time that they are ready to escape, the sperm-cells are so crowded as to press with sufficient force against the walls of the parietal cells to diminish their cavities very considerably (Pl. 4, fig. 24). These cells at the same time absorb much water, and if a ripe antheridium is placed in water, the tension resulting from the combined pressure of the cells within, and the turgidity of the parietal cells from the absorption of water, are sufficient to cause a rupture in the wall of the antheridium. This usually takes place between the two upper cells, the cap-cell being torn in the operation, but sometimes by a rent in the cap-cell only. As this occurs the lower parietal cells become much swollen and press inwards upon the mass of sperm-cells which are thus forced out through the opening. Their discharge is accompanied by a small amount of mucilaginous matter, evidently the remains of the disintegrated walls of the mother-cells. After lying quiescent for a few moments (Pl. 4, fig. 27) the vesicle in which the antherozoid is contained bursts and the antherozoid swims rapidly away with a twisting movement due to its spiral form. It consists of hyaline protoplasm, somewhat flattened and enlarged at the forward end, which sometimes shows two or three indistinct and close coils, the hinder part being composed of one or two open and complete turns of the spiral (Pl. 4, fig. 28). The cilia are numerous, being developed principally on the anterior coils but also extending back to the beginning of the larger ones. They are directed somewhat backward, as is plainly seen in treating the antherozoid with iodine, which causes it to become deeply stained and somewhat contracted and the cilia rigid and sharply defined. The end tapers to a point which sometimes is much prolonged. When the antherozoid has recently escaped, the movement of the cilia is so rapid as to render them almost invisible, but as it dies the movement becomes slower and is then seen to be undulatory, the movement seeming to begin at the point nearest the body and to proceed outward toward the tip of the cilium. This movement continues for some time after it ceases to be strong enough to propel the antherozoid.

It sometimes happens that the antherozoid does not become entirely free from the membrane of the cell in which it lies so that its movements are much hampered, the vibrations of the cilia being only sufficient to cause a rotation of the cell. It may subsequently free itself entirely or it may never escape completely. As the antherozoid swims away, there is seen attached to it a delicate vesicle which absorbs water and becomes much distended. Contained in this are several fine granules, the whole being the remains of the mother-cell of the antherozoid. This vesicle is sometimes attached to the pointed end of the antherozoid, sometimes it adheres for a considerable part of its length.

It occasionally happens that the antherozoids are imperfect in form, the hyaline protoplasm that constitutes the body not being sharply differentiated from the granular protoplasm of the central parts of the mother-cell. In such cases the antherozoid is club-shaped with the cilia at the pointed end, and the movement is less decidedly rotary.

The archegonia, like the antheridia and root-hairs, arise from the superficial cells of the prothallium and are, therefore, morphologically trichomes. Unlike the antheridia they are confined to a special part of the prothallium, being formed only on the lower surface of the cushion of tissue which lies at the bottom of the cleft in the front of the prothallium. If the earlier archegonia are not fertilized, new ones continue to form as long as the prothallium grows, the latter in such cases reaching a considerable size and bearing, sometimes, a hundred or more archegonia. In such cases, the cushion of tissue, elongating with the prothallium, forms a sort of mid-rib leaving the remainder of the prothallium a single layer of cells. In these large prothallia the edges are usually decidedly wavy.

The mother-cell of the archegonium (Pl. 5, fig. 3) is not easily detected at first, resembling in shape and size the other young cells in the vicinity. Careful examination, however, usually makes it distinguishable. Its shape, like that of many of the surrounding cells, is that of a truncated pyramid, the base being at the surface of the prothallium. Viewed from above it appears nearly square. The contents are quite different from those of the neighboring cells. In the latter, the protoplasm together with the chlorophyll-granules and nucleus is confined to the parietal parts of the cells, the center containing only cell-sap; in the mother-cell of the archegonium, on the contrary, the protoplasm appears to be more dense occupying nearly or quite all of the cell. The chlorophyll granules are smaller, less numerous and distinct, while the nucleus is not only larger but nearly central in position instead of lying near the wall.

The first step in the further development of the cell is a slight elevation of the outer wall above the level of the neighboring cells, the upper part of the cell becoming usually more transparent. Next, the cell becomes divided into two unequal parts by a transverse wall; the lower cell undergoes no further change beyond simple division, taking no further part in the formation of the archegonium, but acting in all respects like the vegetative cells of the prothallium. The upper and larger cell next divides by another wall parallel to the first, but more or less convex, the outer of the two cells thus formed containing less protoplasm than the lower and forming the beginning of the neck; the lower, filled with dense protoplasm and containing a large central nucleus, is the central cell from which is finally developed the germ-cell (Pl. 5, fig. 4). The upper cell now becomes divided by a wall at right angles to the longer axis of the prothallium into an anterior and posterior cell; this wall is sometimes vertical, but more commonly inclined backward so that even from the first, the anterior part of the neck is larger than the posterior (Pl. 4, fig. 31, Pl. 5, fig. 2). A wall is next formed at right angles to the first so as to divide the cell into four parts (Pl. 5, fig. 1). These are the beginnings of the four rows of cells composing the neck of the mature archegonium. The protoplasm of these cells is nearly destitute of granules, so that they are nearly colorless, and this characteristic is maintained. Of the four cells into which the primary neck-cell is first divided the two lying in front grow more rapidly than the others, so that the neck very early shows a decided curvature backward, the amount of curvature depending largely upon the degree of inclination of the first formed wall. Each of the four cells next divides by a transverse wall and later by a series of walls parallel to the first (Pl. 5, fig. 2). The first of these walls seems to appear somewhat earlier in the two anterior cells, the two rows of neck-cells developed from these containing, usually, about two more cells than are found in the other two, there being ordinarily six or seven in the anterior, four or five in the posterior rows.

Each neck-cell in the mature archegonium has a distinct nucleus lying close to the wall, the latter being lined with a thin layer of very finely granular protoplasm in which are embedded a few larger granules, some of which show a faint greenish color. With this exception the contents of the cells are perfectly colorless (Pl. 5, figs. 6, 7).

While the neck-cells are growing, the central cell of the young archegonium is also undergoing changes. The wall by which it was separated from the primary neck-cell becomes more decidedly convex and pointed, pushing up between the four rows of neck-cells. About the time that the first transverse septa are formed in the neck-cells, the upper pointed part of the central cell becomes cut off by a septum which is concave upward, from the main part of the cell (Pl. 5, fig. 2). The upper cell becomes the canal-cell of the neck; the lower, the central cell, from which finally the germ-cell is formed. Although a very large number of archegonia in all stages of development were examined, no trace of any further division of either central cell or canal-cell could be detected beyond the presence in the latter of several nuclei, it appearing probable that in this case, at least, the so-called ventral canal-cell of Janczewski does not exist.

In its earlier stages the canal-cell is sometimes quite conspicuous, but as it becomes older its outlines are not so definite. The protoplasm is colorless and densely granular, and frequently several nuclei can be detected but no division-walls, except the first one by which it is shut off from the central cell. It continues to elongate as the neck of the archegonium grows, reaching as far as the base of the upper cells. When the archegonium is ripe, the wall separating the canal-cell from the central cell becomes mucilaginous, and probably also the inner layers of the walls of the neck-cells, in a manner analogous to that described in the case of the antheridium. If now water is applied, the walls of the cells dissolve and the space occupied by the neck-cell becomes filled with a colorless mucilage derived from the disintegrated cell-walls, together with the protoplasm of the cell. This change is accompanied by active movements of the contents of the canal, the movements being very marked and lasting for about a minute. This was observed only in a single instance, but from the resemblance to what takes place in the antheridium, is probably the normal process. After the movements had ceased it was seen that the more solid portions of the contents of the neck had collected in a row of two or three pretty distinct masses, the lower one of which was somewhat rounded, corresponding in appearance with Sach's figure of the central canal-cell (Pl. 5, fig. 6). It is possible that this, which is undoubtedly only part of the contents of the canal-cell, may from its appearance have been considered as a separate cell. There is not always, however, this separation of the granular part of the contents, but in many cases the contents appear the same throughout.

Probably at the same time that the change described in the neck-cells takes place, but which could not be determined with absolute certainty, the contents of the central cell, which have hitherto been uniform, undergo a change. The protoplasm contracts into a spherical mass which does not completely fill the central cell; this is the germ-cell or oösphere. It contains a large central nucleus and in favorable cases a transparent area can be detected lying on the side nearest the neck, this being the receptive spot; the rest of the protoplasm is colorless but densely granular. The central cell increases in size but little from the time it is first formed; it is surrounded by a single layer of small cells cut off from the adjacent cells of the prothallium including the basal cells of the archegonium, which usually becomes divided into two nearly equal cells, but otherwise is unchanged in appearance and easily identified. Thus the basal part of the archegonium is completely embedded in the prothallium, the neck alone projecting beyond the surface.

The neck-cells of the ripe archegonium possess the same property of absorbing large quantities of water that was observed in the parietal cells of the antheridium; and becoming much swollen the pressure exerted upon the contents of the canal is sufficient to force apart the upper neck-cells, which finally diverge widely, allowing the contents of the canal to escape, leaving a clear passage down to the germ-cell (Pl. 5, fig. 7). This process can be easily seen by allowing prothallia upon which there are mature archegonia to remain somewhat dry for two or three days. Longitudinal sections of these being made and mounted in water will be certain to show some archegonia ready to open, and generally within a few minutes sufficient water will have been absorbed to force open the neck and discharge its contents. For a satisfactory study of the development of the archegonium, these longitudinal sections of the prothallium are necessary, archegonia in all stages of development being found in the older prothallia.

The upper cells of the archegonium separate slowly at first, this being accompanied by a slight discharge of mucilage. As water continues to be absorbed by the neck-cells, they become much swollen and the upper cells are torn apart, often with violence enough to detach entirely some of the uppermost ones. At the same time, by the inward pressure, the remaining masses of mucilage are forced out, collecting in masses of some size around the opening of the archegonium (Pl. 5, fig. 7). Besides the granular masses which are mainly composed of the protoplasm of the neck-cell, there is a quantity of viscid, perfectly colorless and transparent matter, whose presence is made evident by the behavior of the antherozoids that come in contact with it. The antherozoids collect in greater or less numbers about the mouth of the open archegonium, their movements being retarded by the mucilaginous matter expelled from the neck, but by far the greater number are not detained by the mucilage, or only temporarily; and of those held, only a very small part ever enter the archegonium. When an antherozoid comes within the immediate vicinity of the archegonium, its movements are very much checked, there being evidently some substance present that interferes with the free movements of the cilia. One may frequently be seen to come to a sudden stop, and after vigorous efforts to free itself, swim away with undiminished vigor. The canal of the archegonium appears to be filled with the same substance, for although nothing is visible the movements of the antherozoids are so much checked that in nearly every case observed, they failed to penetrate to the germ-cell, although making their way for some distance down the neck. This necessitates the fertilization of the germ-cell by a fresh and active antherozoid, as only such would have strength to make its way down to the germ-cell.

The entrance of the antherozoid into the neck of the archegonium was observed a number of times, and in one case one was detected within the central cell. Before entering the movements cease almost entirely for a few moments, and are then resumed, the body being somewhat stretched and the movement slowly rotary; at the same time, by a quick movement of the pointed end of the body, the vesicle is thrown off (Pl. 5, fig. 9).

In the single case in which the antherozoid was observed within the central cell, the form of the antherozoid could not be clearly made out, though the movement of the cilia was plainly seen for several minutes, when it ceased, and the antherozoid became lost to view, presumably fusing with the germ-cell, but its mode of entrance could not be made out. The neck-cells of the same archegonium, examined twenty-four hours later, showed a decided brown color, which was not observed in unimpregnated archegonia of the same age, and the germ-cell had divided (Pl. 5, fig. 10).

In making experiments in fertilization, a number of male prothallia, freed from earth, were placed upon a slide, and with them longitudinal sections of female prothallia, some of which are almost certain to contain ripe archegonia. If the prothallia have been kept somewhat dry for two or three days, especially in warm weather, both archegonia and antheridia will open very soon after they are placed in water. In this way freshly opened archegonia and numerous antherozoids were present upon the slide, and could easily be observed, but although many trials were made, the antherozoids in the great majority of cases failed to enter the archegonium at all.

The prothallia are always strongly dioecious, the male prothallia never bearing archegonia, and the female only in rare cases developing antheridia, and then only in small numbers, and before the archegonia are mature.

Various experiments were made to find out what were the most favorable conditions for growing the spores, and several were more or less successful. The earliest stages can best be observed by placing the spores simply in water, as they are then free from foreign matter; but they do not develop in a healthy manner if left in water, the prothallium becoming very long and slender, the transverse septa being wanting, or only developed at long intervals. Finding that some fern prothallia grew naturally on rotten wood, spores that had germinated in water were transferred to this material and developed male prothallia, but no female ones. Probably further trials might have been more successful. The best results were obtained by sowing the spores in fine earth in shallow earthen saucers which were kept under glass to prevent too rapid evaporation. In cold weather, they were exposed to direct sunlight, but in warm weather were kept partially shaded. Care must be taken not to keep them too wet, for if they are kept soaking wet for a few days they are apt to decay, besides inducing a growth of algae, such as Oscillaria, etc., which sometimes interfere with the growth. In cultures that have been kept for some months, it is almost impossible to prevent the growth of mosses, whose protonema, unless kept down, sometimes interferes with the ferns; but if the prothallia are well established, a little care in removing the mosses from time to time will be sufficient. Severe freezing failed to kill the prothallia, provided care was taken to thaw them out gradually.

Attempts to grow the prothallia in porous pottery met with indifferent success.

All of the prothallia, from which the foregoing observations were made, were grown artificially, none having been met with growing naturally.

Section III. The Embryo.

The first division of the germ-cell is completed within twenty-four hours after fertilization and is effected by a wall (the basal wall) which is slightly inclined to the surface of the prothallium and perpendicular to its longer axis. The basal wall may be inclined either toward the front or back of the prothallium and divides the embryo into two cells, the epibasal lying in front, and the hypobasal behind (Pl. 5, fig. 15). Each of these cells is next divided by a wall (the transverse wall) perpendicular to the basal wall and parallel to the surface of the prothallium, so that the four-celled embryo, seen from above, appears to have only two cells (Pl. 5, figs. 11, 17). Each of the four cells is next divided by a wall (the median wall) parallel to the long axis of the prothallium, so that the embryo now consists of eight cells arranged like the octants of a sphere.

Up to this point, as far as is known, the majority of ferns seem to agree, except as to the relative time of the formation of the transverse and median walls, which appear in different order in different species. As to the further history of the eight primary cells of the embryo, there is considerable disagreement. After repeated examination of a large number of specimens, the following conclusions have been reached with reference to the fern under consideration.

If we examine again the eight-celled embryo, it is easily seen that each one of the cells is nearly tetrahedral in form; that is, the walls that bound the faces that are in contact are approximately plane triangles, the outer wall a spherical triangle. Each of the eight cells thus *has the form characteristic of the apical cell of the mature stem and root.* For a short time these all grow in essentially the same way as the apical cells of these organs, but this growth is checked in all but those two that finally assume the function of these two cells.

Of the four cells first formed, the two lying in front of the basal wall give rise to the first leaf and the stem; those of the hypobasal half of the first root and foot (Pl. 5, fig. 11). Of the epibasal portion, the one next to the neck of the archegonium forms the first leaf, the other the stem; of the hypobasal half, the lower (next the neck of the archegonium) the first root, the upper the foot.

The first divisions are essentially the same in all the octants, though there is slight variation in some cases. The first wall (Pl. 5, fig. 14, 1) is usually parallel to the basal wall, and is soon followed by a second, parallel to the transverse wall; sometimes this order is reversed, but never, so far as could be made out, was the first wall in the octant parallel to the median wall. Before any further segments are cut off from the primary cells (octants), these first segments undergo further divisions. Each one is divided into two cells by a tangential wall, an inner and an outer cell (fig. 13). Each octant now consists of five cells, two inner and three outer, one of the latter being the primary cell which still retains its tetrahedral form. After a segment has divided into an inner and an outer cell, the latter becomes divided into two by a radial wall, but beyond this the succession of walls differs. Of these eight tetrahedral cells, four, one in each quadrant of the embryo, soon lose their primitive form: indeed this sometimes occurs even before the second set of segments is cut off from the primary cells. This is brought about as follows: In one of the primary cells of each quadrant, after the first or second divisions have taken place, instead of new segments being cut off in the same way, a tangential wall is formed, dividing the primary cell into an inner and an outer one. The outer one is divided by radial walls; and the inner, dividing by walls directed in various directions, soon becomes indistinguishable. There are thus left remaining four of the primary cells, as the apical cells of each quadrant. Of these, those of the stem and root remain unchanged; that of the leaf undergoes some further changes, to be presently described; while that of the foot, after one or two more sets of segments have been cut off, is divided by a tangential wall into an inner and outer cell, in the same way described in the other primary cells, and thus ceases to act as an apical cell.

Although the apical cell of the first leaf is at first like that of the other quadrants, tetrahedral, after about two sets of segments have been cut off, no more — or at any rate, no more, as a rule—are cut off from the side parallel to the transverse wall. The succeeding segments are formed alternately from the sides originally parallel to the basal and median walls. By the obliteration of one of the original cells of the leaf-quadrant, and by subsequent growth and consequent displacement of cells, the apical cell of the leaf, as seen from above, occupies nearly the center of the leaf-quadrant (Pl. 6, fig. 1). As a result of the formation of segments in two directions only, the apical cell loses its original tetrahedral form, and approximates the wedge-shaped apical cell of the later leaves. Some time before the embryo is ready to break through the enveloping tissue, a further change takes place in the apical cell of the leaf. It undergoes division, each half assuming the form of the original, and becoming the apical cell of one division of the strongly two-lobed leaf (Pl. 6, fig. 3). The division takes place as follows. The apical cell is divided into two equal parts by a vertical wall. Each of the resulting cells is next divided by a curved wall running from the outer margin of the cell to the wall that belonged to the original cell. There are thus formed four cells, the two central ones being elongated, the others nearly triangular in outline. The former become divided by a transverse wall into an inner and outer cell; the two latter by walls alternately right and left: being, in fact, the apical cells of the lobes of the leaf.

The young leaf grows much more rapidly than the stem, and soon projects beyond it. The multiplication of the cells being greater on the lower side, the leaf begins to curve upward. The cells of the leaf-stalk now elongate rapidly, and after the embryo has broken through the overlying tissue of the prothallium, the leaf pushes up between the lobes of the prothallium, appearing above its surface (Pl. 6, fig. 5).

The apical cell of the stem divides much more slowly, and follows nearly the same plan at first. The segments later divide somewhat differently, the first division wall of the segment being a radial one, and dividing the segment into two nearly equal cells. The stem is very short at the time the embryo breaks through the prothallium, but the apex is more decidedly conical than is the case in the mature plant.

The apical cell of the foot soon becomes obliterated by a process entirely similar to that already described, but the cells continue to multiply rapidly with no regular order. By means of the foot, which when complete is large and rounded in shape, the embryo is kept in close connection with the prothallium, and by means of it the embryo is nourished until the first leaf and root are developed.

After the first segments are cut off in the apical cell of the root, it usually continues to act for some time like that of the stem, the first wall of the segment being radial instead of tangential. Of the subsequent divisions, the tangential are much more numerous than the radial. After a varying number of segments have been cut off as described, a wall is formed in the apical cell parallel to its outer surface; this is the first cell of the root-cap. This cell becomes divided by a vertical wall into two, and next by a wall at right angles to the first, into four. Others are formed later, but only in two planes, there being no tangential walls formed (Pl. 5, fig. 16, Pl. 6, figs. 2, 4). From this time on, each cycle of segments in the apical cell consists of four cells. The development of the root varies greatly at the time the embryo breaks through the prothallium. In the majority of cases examined (fig. 2) the root was much shorter than is usually figured in other ferns at the same stage, and this corresponds with the comparatively late appearance of the first cap-cell; but it was not uncommon to find specimens, in which the root has attained considerable size at this time, and indeed is the first part to break through the prothallium. The root-cap in such cases is composed of several strata, and the first cap-cell must have been formed much earlier.

Shortly before the embryo breaks through the prothallium, the first traces of the primary fibro-vascular bundles are formed (Pl. 6, fig. 2). In the central row of cells, in each of the four members of the embryo, is formed almost simultaneously, a series of longitudinal walls, by which there is formed a central bundle of narrow cells, the procambium of the bundles; hence the primary fibro-vascular bundles must be regarded as distinct, and entirely independent of each other. Of these four bundles, that of the foot is short, and ends blindly within that organ, but the others continue to lengthen with the growth of the organ to which they belong, and shortly after the breaking through of the embryo, the permanent elements of the bundle begin to develop. The stem grows slowly, but the leaf and root with great rapidity; the former, even before the emergence of the embryo, being evidently two-lobed. The apical cells of these lobes also undergo bipartition, so that all the divisions of the primary frond are the result of strict dichotomy. Small glandular hairs appear upon the young leaf, and root-hairs from the surface cells of the root, even before any definite epidermis can be detected. The root rapidly grows downward, the first leaf enlarges and the prothallium, which had hitherto nourished it, withers away and disappears leaving the young plant firmly fastened to the ground.

The primary bundles are arranged like a cross, two of the arms being longer. The longer arms are the bundles of the leaf and root. The first tracheary tissue begins to form about the time that the embryo breaks through the prothallium. Faint thickenings make their appearance on the walls of certain of the procambium cells which soon assume the form of scalariform tracheids. The pits are shorter than in the later tracheids, and there are usually two or three rows. There are no true vessels, the tracheary tissue consisting throughout of single cells or tracheids.

As the leaf-stalk lengthens, its primary tracheids continue to form through the center of the bundle, and around them other spiral ones are developed, growth proceeding from the center toward the circumference of the bundle. The other elements of the bundle follow, but are never perfectly differentiated, consisting simply of elongated, narrow cells with thin walls and colorless contents. These do not taper at the ends but are abruptly truncate, the septa being more or less oblique. The same form of bundle is found in all the earlier leaves, none but spiral tracheids being found in them. The later tracheids are broader than the primary ones and the spirals not so close together. Although there is no distinct bundle-sheath, the bundles are pretty well defined on account of the large size of the cells of the surrounding parenchyma, which are very different from the narrow cambiform outer cells of the bundle.

As might be expected, the veining of the leaf is dichotomous. The bundle in the stalk forks at the base of the lamina, sending a branch to each lobe; these branches fork, and their divisions also; the last veins thus formed may or may not divide once more.

In the first root, the primary tracheids are central, as in the leaf, and the development proceeds outward. The tracheids are all short and pointed, forming a cylinder which constitutes the greater part of the bundle. They are marked with transversely elongated pits, or with shorter ones placed in two or three rows. The remainder of the bundle consists of one or two layers of narrow cells surrounding the tracheary tissue, their cells having more or less oblique transverse septa. The ground tissue of the root consists of about four layers of large parenchymatous cells, about three times longer than broad. In those nearest the base of the root, chlorophyll is present, but it is wanting in the subterranean parts. The cells of the outer layer differ but little in form from those of the ground tissue, except in being narrower, but their walls soon become brown and thickened, and, finally, the contents disappear, leaving them dry and scaly. From the outer surface of the cells abundant root-hairs are formed.

The second root, like all the subsequent ones, is endogenous in its formation. The apical cell is formed in the tissue at the base of the second frond near the point at which the bundle of the leaf connects with that of the stem. As the root grows, its central cells become divided by longitudinal walls into a cylindrical mass of cells, the procambium of its fibro-vascular bundles, its growth beginning with the cells that lie in contact with the bundle of the stem. The formation of the second root begins while the second frond is still young and before it is unrolled. The root breaks through the base of the leaf about the time that the frond unrolls. The tip of the root contains enough chlorophyll in very fine granules to give it a decided green color; this, however, not extending for any great distance, the cells nearer the base being nearly colorless. The first development of permanent tissue in the bundle takes place at two points instead of one. Two rows of narrow spiral tracheids are formed simultaneously near the foci of the elliptical bundle, and the development of the tracheary tissue proceeds inward. The rest of the bundle is composed of narrow elements similar to the corresponding tissue of the first root.

The bundle of the young stem is solid instead of being a hollow cylinder as in the mature plant. This is partly composed of scalariform tracheids which are short and pointed and rather broad. There are also spiral and reticulate ones, especially in the center of the bundle. The bundle anastomoses with the base of that of the first frond, the tracheary tissue of the two bundles being in contact. The bundle runs toward the second leaf into which it sends a branch, but tracheary tissue is developed in the stem-bundle beyond the point of contact of the two bundles before any tracheary tissue is developed in the bundles of the leaf. As in the case of the other bundles, no other tissue than the tracheary is completely differentiated.

The procambium of the stem-bundle can be traced nearly to the apex of the conical growing point which soon becomes so covered with the broad scales that it is often difficult to get at it.

The young plant grows rapidly. By the time that the third or fourth leaf is fully developed, the stem has assumed some size and the bundle running through it has become sharply differentiated by the formation of a bundle-sheath whose cells assume a brown color. New roots continue to form endogenously from the bases of the young fronds, the formation beginning before the leaf is fully grown.

The new leaves arise from segments of the apical cell of the stem, and up to the fifth or sixth and probably until the stem reaches its permanent form, the apical cell undergoes bifurcation so that at an early period they consist of two nearly equal lobes. Just how far the subsequent branching of the leaf is due to dichotomy is difficult to determine, but probably in the later formed fronds of the young plant it does not continue beyond the first division, the later divisions, as in the fronds of the mature plant, being monopodial.

A cross-section of the stem of a plant with three leaves completely developed showed that the stem-bundle was elliptical in outline. The center was occupied by a mass of elongated parenchyma cells lying outside of which was a mass of short spiral or reticulate tracheids. Next followed two or three layers of elongated cells much like those occupying the center of the bundle, and surrounding the whole a bundle-sheath formed of narrow cells with brown walls. From the stem-bundle the bundles going to the leaves and roots branched off, their bundle-sheaths being continuous and the tracheary tissue connected.

The stalks of the first three leaves are provided with a single axial bundle; but in the fourth, as in the mature leaf, there are two, one on each side of the deep groove in the front of the stalk. These two bundles are separate nearly or quite to the base, the stem-bundle being deeply cleft at the point where they issue from it. They are nearly round when seen in cross-section, the tracheary tissue being arranged in a band consisting sometimes of a single row of spiral tracheids, only four or five in number, the arrangement recalling that found in the older roots. The rest of the bundle is made up of elongated cells with rather thick walls which appear to swell slightly in water. The whole is surrounded by a sheath.

The number of roots exceeds that of the leaves, there being six fully developed roots in a plant in which the fourth leaf was not fully grown, besides several that were not fully developed.

Section IV. The Leaf.

The leaves arise from single segments of the apical cell of the stem. The first indication of the young leaf is the elevation of the surface of the segment, the apical cell of the leaf being formed very early from one of the surface cells. A wall is formed in this cell inclined to its outer wall so as to meet one of the lateral walls. This is probably followed by a second wall inclined to the first, and meeting it so as to include a wedge-shaped cell, the apical cell of the leaf. From this time the growth of the leaf is dependent upon the further development of this apical cell, which divides by walls directed alternately right and left into two series of segments. The early growth of the apical cell is rapid, soon resulting in a flattened cone with a broad base, the side in contact with the stem being more flattened than the outer face, which grows more rapidly, so that the young frond soon begins to bend inward over the end of the stem. This inequality becomes more and more strongly marked as growth proceeds, finally causing the frond to be closely coiled as is well known in all ferns.

The leaf-stalk develops at first much more rapidly than the lamina, which remains very small, proportionately, until the latter part of the summer previous to its unfolding, when it undergoes a great increase in size; the unfolding of the leaf being little more than an expansion of parts already formed, this process taking place with extreme rapidity in strong contrast to the extraordinarily slow development of the earlier stages of the leaf.

The apical cell of the leaf (Pl. 6, fig. 7) is wedge-shaped, differing, therefore, in appearance as seen from different directions. The segments are formed by walls parallel to the lateral faces. Each segment is first divided into two cells by a transverse wall; the main fibro-vascular bundles of the leaf being developed from the inner of the two cells, the mesophyll, and the epidermis from the outer. The outer cell is next further divided by a wall parallel to the primary wall, and these two cells by walls parallel to their outer surfaces, these outer cells constituting the marginal epidermis. In the older leaves these marginal cells, although increasing rapidly in breadth, undergo no further division, the rest of the epidermis arising from the cells lying within these by walls parallel to the surface of the leaf. In the very young leaf, before there is any differentiation of stalk and blade, the growing point is thicker and the marginal cells early undergo division by walls parallel to the surface of the leaf.

Longitudinal walls are formed in the inner cells so as to transform them into a cylindrical mass of cells, those in the center being narrower and forming the procambium, the others the young ground tissue and epidermis. In the blade, all of the structures developed from the central cells remain as the rachis, but in the petiole it is impossible to discriminate between the ground tissue and epidermis developed from these cells and those from the outer ones of the segments. The cells of the procambium (Pl. 6, fig. 7) soon become easily recognizable by their greater length and more transparent contents. In the lower part of the leaf two parts can be distinguished, separated by a mass of shorter cells and these can be traced to the stem-bundle with which they are united, one coming from each side of the foliar gap, or opening in the stem-bundle opposite the insertion of the leaf.

The differentiation into petiole and blade is caused by the lateral growth becoming more strongly marked in the latter, the cells dividing rapidly by walls perpendicular to the surface of the frond, this being very strongly marked in the older leaf.

As growth continues, the young ground-tissue of the petiole begins to show a division into two portions: the true fundamental tissue and the hypoderm. The cells forming the latter are much narrower than those of the former and contain less chlorophyll, so that they are easily distinguished from the parenchyma lying beneath them at an early stage. They have oblique end walls, and increase rapidly in length, the walls also increasing in thickness and finally becoming dark brown. When the hypodermal cells are completed they form a sort of fibrous tissue. Outside of the hypodermal cells there is a single layer of epidermal cells, differing from them in their greater transverse diameter, but being shorter, resembling in shape more nearly the inner ground tissue cells. On the older basal portion of the stipe, the epidermis, together with its appendages, hairs and scales, becomes dry and brown, forming with the hypoderma a sort of cortex protecting the inner soft parenchyma. No stomata are developed from the epidermis of the petiole or rachis.

By the time that the ground tissue becomes recognizable as such, the formation of vertical walls in its cells ceases, the subsequent increase in the number of cells being caused by transverse walls only, resulting in the formation of regular vertical rows of cells. In the younger parts of the petiole these cells are often much broader than long, owing to the rapid division. They contain fine granular protoplasm and distinct chlorophyll granules which are most abundant in the center of the cell, surrounding the large round nucleus. The subsequent thickening of the petiole is brought about by the enlargement of these cells which ultimately also increase very much in length. As the cells enlarge, they lose the chlorophyll which seems to be gradually replaced by starch. Even when colored with chlorophyll, the action of iodine caused the chlorophyll bodies to turn a dark bluish color, while in the older cells, from which the chlorophyll has entirely disappeared, the characteristic blue color is produced in the granules, which seem now to have the whole of the chlorophyll replaced by starch, appearing, indeed, like ordinary starch grains. A similar, apparent transformation of the chlorophyll bodies into starch grains was observed in the prothallium.

The fibro-vascular bundles of the petiole are ribbon-like, the transverse section being several times longer than broad. Before any markings are evident on the walls of the tracheids, their position can be easily made out by the greater size and transparency of the procambium cells from which they are to be formed. These cells form a band running through the center of the bundle, and curving at the ends (seen in transverse section). The first tracheids are formed at the points of curvature on the inner side of the central band of cells. From these the formation continues, following the course of the band. These first ones are short and marked reticulately with close coiled spirals. The secondary tracheids are mainly scalariform. As already noticed the cross-section of the bundle is much longer than broad, the proportion being about ten to one. It is very slightly curved and only about half as broad in the middle as at the ends; the outer end being the broader, and being also less obtuse. The bundle is surrounded by a bundle-sheath composed of small cells whose walls are colored brown. This is more plainly seen in the upper part of the petiole where the bundles are somewhat smaller. When the petiole becomes dry the cells of the bundle-sheath split through the middle, so that the bundle separates from the ground tissue. Lying inside of the bundle-sheath, and surrounding the tracheary tissue, are from six to eight rows of cells in the lower part of the petiole, a somewhat smaller number in the bundle of the more slender upper portion. These vary much in size, are of prismatic form with moderately thick colorless walls, and no intercellular spaces. In the lower part of the bundle these are filled with starch but in the upper parts are nearly destitute of granular contents. The central part of the bundle is occupied by the tracheary tissue, mainly composed of the large secondary scalariform tracheids. They are strongly angular, the walls between neighboring ones being straight. The division walls are very sharply defined and in the older bundles often assume a clear yellowish brown color. In the narrower part of the bundle they form a central band of varying width, the tracheids also differing a good deal in diameter: but in the enlarged ends of the section the band of tracheary tissue, instead of terminating at the end, is bent on itself forming often a double band. This is more strongly marked in the outer end than the inner. The space between the two bands of tracheids at the ends of the bundle is filled with cells much like those that lie just outside them, but in the larger end they are somewhat smaller. In some places small cells lie between the tracheids, which in the parts of the petiole that survives the winter become filled with starch. Among the tracheids near the ends of the bundle, there may sometimes be detected a group of smaller and more rounded ones,—the primary tracheids.

(Pl. 6, fig. 9. Inner end of a transverse section of the bundle of the petiole: *xy*, tracheary tissue; *ph*, phloem; *sh*, bundle-sheath. The band of tracheary tissue is not as strongly curved as usual.)

The first leaf developed from the end of a stolon shows striking embryonic characters, the whole leaf resembling in many respects the early ones of the germ-plant. The groove in the front of the petiole is not so strongly marked as in the later leaves, the petiole being nearly cylindrical; the hypoderm is reduced to form two to three rows of cells, and these are not so well differentiated as in the later leaves. The fibro-vascular bundles differ much, resembling almost exactly those of the third and fourth leaves of the germ-plant, being oval in section instead of elongated, and the elements of the bundle are less perfect than in the later leaves.

As is the case in the early leaves, the two bundles of the petiole in the mature leaves of the plant unite in the rachis into a single bundle, by a straight band of tissue forming so as to connect their inner edges. The bundle shows in its earlier stages four points at which the formation of tracheary tissue begins, corresponding to the same points in the separate bundles lower down. A cross-section of such a bundle, especially when treated with potash, shows clearly the position of the different elements of the bundle while still incomplete. The central procambium cells, from which the tracheary tissue is to form, become much clearer than the outer ones, and are seen to be, for the most part, larger. The primary tracheids appear almost simultaneously at the four points mentioned, and are easily recognized by their thickened walls.

Following these a number of small tracheids are formed around the border of the central mass of procambium, the development proceeding thence toward the center. As in the bundles of the petiole, the bulk of the tissue lying between the tracheids and the bundle sheath undergoes little further change, the sieve tissue being even less perfectly developed than in those parts. The development of the pinnae begins with the formation of segments by the apical cell of the leaf, after the blade becomes differentiated. Each segment gives rise to a pinna, which in turn becomes deeply pinnatifid. The formation of the pinna begins by the marginal cells of the segment growing more rapidly than those lying within them, thus causing the outer parts of the segment to project. These marginal cells multiply rapidly by longitudinal walls which repeatedly bisect them. Frequently, by one of the marginal cells in the middle of the young pinna becoming divided by an oblique instead of vertical wall, a triangular marginal cell is formed which becomes the apical cell of the pinna and divides in the same way as the apical cell of the leaf. On account of the difference in age of the segments from which they arise the pinnae are not opposite, but alternate. Whether or not an apical cell is always formed in each pinna is questionable; at any rate it cannot always be detected in the pinna when first formed. Sooner or later it is obliterated, in the same way as that of the prothallium, by a transverse wall, which is followed by a second wall at right angles to the first, the two marginal cells thus formed acting from this time on in all respects like the others.

In cases where an apical cell is formed in the pinna, the segment divides, as in the apex of the frond, into two cells, an outer and an inner, the latter forming the midrib or secondary rachis, the former the mesophyll and epidermis, as well as the veins. Each outer cell divides into two by a wall parallel to the primary wall, and these in turn divide farther into an inner and outer cell, as was the case with the original segment (Pl. 6, fig. 7). A single row of marginal cells is thus formed about each lobe of the pinna, which continues to undergo the same divisions. The lobes of the pinna arise from it in precisely the same way that the pinnae are formed from the frond.

The cells lying immediately within the marginal cells divide by walls parallel to the surface of the leaf, so that a flat mass of cells is formed of which the outer layers are prismatic, forming the young epidermis, the inner ones polyhedral constituting the mesophyll. Up to this point the cells of the young lobes resemble each other, all containing finely granular, colorless protoplasm and having a large nucleus.

The cells of the young secondary rachis divide also by walls parallel to the surface of the leaf so as to separate them into a central cylinder, which is transformed by longitudinal walls into the procambium of the bundle, and the overlying ground-tissue and epidermis. The central cells of the young lobes become also divided by a series of longitudinal walls into a mass of narrow procambium cells running nearly to the tip of the lobe. The lateral veins are formed in acropetal succession, but do not begin to form until the lobe has reached some size. If the lobe has a definite apical cell, each lateral vein probably corresponds to each segment cut off from it; but when there is no apical cell, as is much more frequently the case, it is impossible to trace them back to a single cell. They arise from rows of cells in the young mesophyll extending from the midrib to the margin. These cells become divided by longitudinal walls so as to form the procambium of the young vein. The end of the midrib sometimes forks, so that there here remains a trace of the dichotomous branching of the veins of the earliest leaves. Cases where several veins appear to arise by dichotomy are sometimes met with, but these are exceptional, and probably never occur in fully developed fronds.

The formation of the young epidermis, ground tissue and procambium, is completed the year before the fronds unroll, and in the stalk the bundles develop a considerable part of the tracheary tissue; but it is not until the fronds begin to unfold that the different tissues become fully developed: and after this begins the process is a very rapid one.

The young epidermal cells increase very much laterally but with little increase in depth, so that they become tabular with extremely irregular sinuous outlines (Pl. 6, figs. 10–14). The mesophyll, which is at first composed of polyhedral cells with no intercellular spaces, becomes very loose by the formation of intercellular spaces arising from the unequal growth, and separation of the cells. The fibro-vascular bundles develop their different tissues now, stomata are found in the epidermis of the lower surface of the frond, the frond becoming in the meantime completely uncoiled, and the leaf is complete.

The formation of a stoma is preceded by the cutting off of a preliminary cell (Pl. 6, fig. 12), from which the mother-cell of the stoma is subsequently formed. This first wall is V-shaped, or nearly semicircular, and is soon followed by a similar but smaller one nearly parallel to it (fig. 10). The cell cut off by this second wall is the mother-cell of the stoma (fig. 10 *y*). The protoplasm in this cell is more dense than in the surrounding cells, the nucleus is well-marked, but the chlorophyll-granules, which are very definite in the ordinary epidermal cells, are almost wanting, or at least, very poorly defined.

A vertical section of the mother-cell at this time shows that it is somewhat elevated above the surrounding cells, and is also somewhat deeper. The mother-cell is first divided by a longitudinal wall, parallel to the axis of the lobe of the pinna, the nucleus showing evident signs of division before any wall can be detected. By the time that the division wall is complete, the stoma has assumed nearly the oval form of its completed condition, but the space between the guard-cells is wanting. This is formed by the division walls splitting through the middle. Vertical sections show that the air-space beneath the young stoma is small, but as the leaf grows, the space rapidly enlarges and finally reaches considerable size. In the meantime, the walls around the opening of the stoma become thickened, and the whole stoma enlarges. The chlorophyll-granules, which are indistinct in the young stoma, increase rapidly in size and number, and fill up nearly the whole of the guard-cells. Those in the mature stoma are elongated-kidney-form, but the ends are only slightly rounded, so that the whole stoma is almost perfectly elliptical in outline. The accessory cell, which at first had a smooth outline, acquires the sinuous outline of the other epidermal cells, and can only be distinguished from them by its position.

There are produced from the surface cells of the young leaf great numbers of hairs. In the youngest leaves they are mostly glandular, the terminal cell being much enlarged and pear-shaped, and filled with a densely granular but colorless mucilaginous secretion which is somewhat troublesome in the study of the young leaf. Such glandular hairs can be traced up to within a very short distance of the tip of the leaf, before any of the tissues are clearly differentiated. On the older parts of the leaf, when the epidermal cells have assumed their characteristic form, but before they are full grown, both simple and glandular hairs are developed, but the latter differ from those just described in regard to the contents of the terminal cell, the contents being dark brown and apparently resinous, instead of colorless mucilage. When the leaf is unfolding, but not fully grown, these glandular hairs are so numerous as to give a rusty appearance to the petiole and lower surface of the leaf.

Besides the hairs, there are formed upon the basal parts of the petiole of the young leaves, and also upon the growing point of the stem, large numbers of scales, whose first formed cells elongate rapidly, no longitudinal walls being formed in the extreme end ones, so that the scale, which is broad at the base, tapers to a point consisting of a single cell, or more commonly a row of two or three, which become extraordinarily elongated. The terminal cell develops a gland filled with mucilage, but the growth of the scale continues long after the gland has been destroyed, and the cells supporting it dried up. The scale grows at the base which becomes broadly cordate, the cells there undergoing rapid division. The upper cells gradually die and lose their contents, becoming dry and brown, and finally the whole scale dries up, so that they form a thick brown chaff clothing the bases of the petioles.

In the young plant the leaves have the one-third arrangement, but in the older ones they are so crowded that it is somewhat difficult to make out their arrangement; but with care it may be seen that it is the same as described by Hofmeister for *Aspidium Filix-mas*, *A. spinulosum*, and *Asplenium Filix-foemina*, the five-thirteenth arrangement. That is, the angle of divergence is five-thirteenths, and the fourteenth leaf stands above the first, etc. On examining a plant at the end of the season, it will be found that not only are the leaves for the following year plainly evident, but also those of the year after. In a small plant that had only unfolded four leaves the previous summer, there were easily seen fourteen young leaves in various stages of development, and this simply by drawing back the outside ones. The outermost ones have the broad base of the petiole almost completely formed in the autumn, the frond being very small and closely coiled. It generally happens that some of these outer ones do not develop the frond at all. The inner ones rapidly become smaller, and it is not easy to tell just how many are to develop the next season. Indeed it sometimes happens that if the first set of fronds is prematurely destroyed, others may develop later that ordinarily would not have done so until the following season.

Each year there is found a circle of fronds which grow nearly upright, but the tips bend slightly back, so that the group has the form of a deep vase, giving the plant an extremely elegant appearance. These fronds are all sterile and are ordinarily about one metre in height, but may reach twice that, or even more. The frond is pinnate, the pinnae being deeply pinnatifid. It increases in breadth from the apex to a point below the middle when it becomes narrower tapering thence to the stipe, the lowest pinnae being extremely reduced. The lobes of the pinnae are entire except in the first aërial leaves that are produced by the stolons, in which the pinnae are not so crowded and the lobes broader in proportion and slightly dentate, recalling somewhat the earlier leaves of the germ-plant. The lobes of the pinnae of the adult leaf are broadly lanceolate, the pinna being cleft almost to its rachis, and each lobe is provided with a mid-rib, which usually forks at the apex and is provided on each side with from eight to ten simple veins which extend to the margin. The hairs developed upon the young frond disappear, leaving it almost completely glabrous.

Specimens brought into the house in April, after remaining stationary for about two weeks, began to unfold their leaves and, in measuring one week after, it was found that they had reached a height of sixteen inches, so that it can be readily seen that the complete unfolding of the leaf would take but a very few weeks.

The fertile fronds begin to unfold about two months later, but their growth is slower, the development of sporangia beginning very early and new ones forming up to the time that the leaf is full grown. The fertile fronds are very much smaller than the sterile, and grow rigidly upright among them, from two to six being ordinarily produced by each plant annually. They seldom grow more than one-half metre in height, and the pinnae are very much contracted, probably on account of the great draft made upon the frond from the excessive production of sporangia. When mature they are dark, almost blackish green in color, and the margins of the pinnae so strongly revolute as entirely to conceal the sporangia. The segments are scarcely separated in the young frond, but there are constrictions between them so that the pinnae have a beaded appearance. Each segment (Pl. 7, fig. 28) has but five veins, a mid-vein and four lateral ones, none of which run completely to the margin. The upper half of the lobe is composed of but one layer of cells, acting as an indusium. A transverse section of the young pinna (Pl. 7, fig. 10) shows that not only is the margin strongly revolute, but that it is folded on itself once, and sometimes twice. Unlike the sterile leaves which decay in the autumn, the fertile fronds, although becoming brown and dry, remain standing through the winter, owing to the stout and firm stalk. In these dried fronds the pinnae often flatten out, and their segments become separated so as to facilitate the dispersion of the spores.

Section V. The Stem.

The growing point of the stem is completely concealed by the young leaves which meet over it, and in addition to this the numerous glandular scales interfere seriously with its study. Unless care is taken, it is an easy matter to confound one of the young leaves with the apex of the stem, for when seen from the side, being conical in form and having a definite apical cell, the resemblance is quite marked. The apex of the stem itself (Pl. 7, fig. 1), when a section passes directly through it, is seen to be much broader than the young leaves. On account of the dense contents of the cells, the primary meristem is difficult to study unless some method of clearing the tissues is employed. The ordinary potassium hydrate solution will usually answer, neutralizing when necessary with acetic acid.

The apical cell (fig. 1, *a*), whether seen from the side or from above, appears triangular, being, in fact, a tetrahedron. Segments are cut off from the lateral faces in regular succession, the direction of the spiral being usually from left to right. Each segment is first divided into two cells by a longitudinal wall at right angles to the lateral wall of the apical cell. Each of these cells is next divided by a transverse wall into an inner and outer cell (fig. 1), and subsequently each outer cell is divided into two by a longitudinal wall parallel to the lateral wall of the apical cell. Each original segment is thus divided into six cells, two inner and four outer ones. From the inner cells the plerome cylinder is formed; from the outer the periblem and the dermatogen. This latter (figs. 1, 2, *x*) results from a series of walls formed in the outer cells parallel to their outer walls.

The inner cells of the segments increase rapidly, the divisions being mostly longitudinal, so that the lateral growth of the segment is much greater than the longitudinal, and the diameter of the stem is rapidly enlarged, so that the end has the form of a cone with broad base and obtusely angular apex.

The outer cells are at first narrow, as seen from the side, being really tabular; later, losing this by divisions perpendicular to the broader faces of the cells.

The mass of meristem, resulting from these divisions, is composed of small, polyhedral cells of about equal transverse and longitudinal diameters, filled with densely granular protoplasm and provided with a distinct nucleus. Very early, a careful examination shows a distinction between the cells developed from the inner cells of the segments and the outer ones. The former are rather longer and their length somewhat greater in proportion to their breadth. These inner cells, which form the plerome in the stem of the mature plant, now become separated into two parts: an inner one which retains for some time its original character and an outer layer whose cells become divided by a series of longitudinal walls into a mass of long, narrow procambium cells. This procambium cylinder is not continuous, but is interrupted at intervals corresponding to the position of the leaves, by spaces in which the cells resemble those of the inner part of the plerome cylinder. These are the foliar gaps, and through them the inner part of the plerome, which forms the medullary parenchyma of the stem, is joined to the periblem from which the cortical parenchyma and hypoderm arise. The procambium has thus the form of a hollow cylinder, with openings at regular intervals, and, as the procambium develops into the elements of the complete bundle, the whole assumes the form of a cylindrical net; apparently formed by the union of separate bundles, but being strictly a single bundle.

Shortly after the procambium begins to form, the central part of the plerome begins to show the formation of the cavities that characterize the central parts of the stem. At certain points the cells become longer and their contents less dense, so that the places appear more transparent than the surrounding tissue. The cells cease to divide, or at least do so more slowly than the surrounding ones. By the rapid growth of the surrounding tissue and the consequent widening of the stem, certain of these cells are torn apart, leaving intercellular spaces that become rapidly larger as the stem widens. These spaces are bounded by loosely arranged cells whose free ends are rounded and with nearly colorless contents containing a few definite granules and a distinct nucleus. From these cells trichomes of different forms are developed. These may be in the form of simple hairs or scales of considerable size. Sometimes, but not very often, they may be tipped with a pear-shaped glandular cell, filled with dense granular mucilage.

The mass of trichomes filling up the cavity now dries up, and the cells bordering them have their walls somewhat thickened and changed to a brown color. Thus, there are formed large air spaces distributed through the stem. Very often these communicate with the spaces between the bases of the leaf-stalks and the stem, by the destruction of the intermediate tissue, brought about in the same way as the formation of the cavities themselves, the cavities thus being brought into communication with the external air. The communication between the inner and outer cavities takes place through the foliar gaps. Finally, the cells about the cavity acquire thicker walls, which are at first yellow in color, but finally dark brown, forming an imperfect sclerenchyma.

The remainder of the medulla develops into a mass of parenchyma, densely filled with starch. The walls gradually become thicker and develop simple pits.

The periblem, which has rather longer cells, separates into two portions, but not until a later period. Its cells become longer and finally several of the outer layer become still longer, their walls also becoming thicker and the contents less opaque. These constitute the hypoderm, and finally become very sharply separated from the underlying cortical parenchyma. Their lateral walls are somewhat uneven, and all the walls swell up more strongly on the application of potash than those of the parenchyma. The walls of the hypodermal cells next assume a yellow color, which becomes later much darker and the wall finally develops pits which extend to the intercellular lamella which is very clearly defined and appears darker than the rest of the wall. This sclerenchyma, although well-developed, does not attain as perfect a form as is found in some other ferns.

The epidermis of the stem never reaches any degree of perfection, as only a very small part of the surface of the stem is uncovered, and none of it in direct contact with the air. Whatever epidermis there is soon dries up and becomes brown like that of the root.

On account of the foliar gaps, as well as the attachment of the bundles from the leaves, roots and stolons, the separate parts of the stem-bundles are usually very irregular and run, for short distances only, in a vertical direction.

The first permanent tissue to appear in the bundle is composed of small tracheids near the foci of the bundle which is elliptical in section. Those at one focus, and these appear rather earlier than at the other, are spiral or reticulate, although they are often scarcely to be distinguished from the later scalariform ones. Those at the other focus are not to be distinguished in appearance from the other tracheids, except that they are smaller than most of them. In the completed bundle they are indistinguishable.

The large scalariform tracheids, making up the bulk of the xylem, are larger than are found elsewhere in the plant. The cells from which they are formed are broader than those of the rest of the procambium, but are not very long. Their ends are at first simply oblique, but as growth continues, they become slightly curved, and each cell somewhat spindle-shaped, and strongly prismatic from the pressure of the neighboring cells. In the earlier stages, before any traces of the markings on the walls are distinguishable, the cells contain abundant protoplasm, in which are embedded numerous coarse granules, and a moderately large oval nucleus. Previous to the formation of the scalariform markings, the contents become somewhat clearer, owing to a partial disappearance of the granules. The markings first appear as faint transverse ridges on the walls that are in contact with another tracheid, corresponding ridges appearing each side of the wall. These soon become thick enough to show that they end at the angles where the tracheids meet, and enclose long, narrow, transverse pits, or spaces where the wall is not thickened. This process begins with the cells lying next the primary tracheids, but after the first begin to form, the remainder of the xylem develops with great rapidity, and almost simultaneously. The ridges separating the pits soon begin to show an inequality in the thickening. At points where they touch the division wall they increase but little in breadth after they are first formed, but as they increase vertically in thickness, they also increase in breadth, until at a point about half-way up they reach a breadth of about twice that at the base. From this point they narrow again, so that a transverse section of one of these bars is nearly rhomboidal. In this way a pit is formed broader at the bottom than at the top, or funnel-form, the broad end of the funnel being in contact with the wall separating the tracheid from its neighbor.

The development of the sieve-tube begins shortly after that of the large scalariform tracheids, and in some respects resembles it. The cells of the procambium, from which the sieve-tubes originate, are uniform in diameter and have squarer ends than the young tracheids, so that the separate elements of the sieve-tubes are more nearly cylindrical than the tracheids. They occupy an irregular area at each end of the bundle, and can be best seen in a section passing through the major axis of the elliptical bundle. Their contents are colorless and more finely granular than those from which the tracheids arise, and the nucleus is not so readily seen. The sieve-discs are more abundant in the lateral walls, and are developed almost simultaneously in all.

Faint, transverse ridges appear upon the lateral walls, much as in the young scalariform tracheids, but they are broader and not so close together, so that the spaces or pits enclosed by them are larger. The bars are frequently somewhat oblique, so that they anastomose to some extent, making the distribution of the pits or young sieve-discs irregular. As they become older these thickened bands become more strongly marked, but the thickenings are uniform, so that the sieve-discs do not present a bordered appearance, although sometimes, owing apparently to a slight rounding of the outer surface of the thickened ridges, the outline of the sieve-disc is not as clearly defined as when the breadth of the band is absolutely uniform. Corresponding thickenings are formed on the opposite sides of the wall, and probably fine pores are developed in the lateral sieve-plates, but this could not be proved. In one case, an oblique wall, which separates the ends of two neighboring tubes, and was very strongly inclined, showed several very sharply defined pits, which appeared to penetrate the wall and thus to throw the cavities of the adjoining tubes into communication. The complete tubes are seldom perfectly straight, the lateral walls being curved, especially at points where the bundle is bent.

The remaining procambium undergoes little change, retaining the form of thin-walled parenchyma occupying the spaces between the tracheids and outside of the sieve-tubes. Two or three rows remain, forming a ring inside the bundle-sheath which differs from them mainly in the walls of its cells being brown, and the cells flattened laterally. As the tracheids become old, their walls often become yellow.

The complete rhizome is comparatively slender, being only about two centimetres in diameter; but, on account of the persistent bases of the petioles, it appears much thicker, often ten centimetres or more. These overlapping leaf-bases give it a bulb-like appearance, as those of several years remain attached. The rhizome is either upright or inclined at the base, and may reach a length of twenty to thirty centimetres, or even more in old plants. The oblanceolate leaf-bases are about four centimetres long by one centimetre in breadth and one-half centimetre thick. They project above the young leaves and thus protect them before they are ready to unfold.

With a little care, portions of the net-like, fibro-vascular cylinder of the stem can be separated, as like the bundles of the leaves, it is sharply differentiated and readily comes away from the surrounding parenchyma. The bundles are firm and woody in texture and the meshes of the net nearly rhombic, about one-half centimetre in length. From the lower angle of each mesh, two bundles, one on each side, are sent to the leaf, there being a leaf opposite each foliar gap.

Below the leaf-bundles, or sometimes connected with them, the bundles of the roots join the stem-bundle, there being usually in the older parts several roots at the base of each leaf. There are no bundles running through the medulla.

Connected with the rhizome there are usually to be found numerous long and slender stolons, which under favorable circumstances appear above ground and develop a crown of leaves.

They arise near the bases of the leaves, and in almost any plant numbers may be met with ranging in size from one-half centimetre in length to twenty or thirty centimetres or more, and apparently remaining dormant for an indefinite period, as the number of undeveloped ones far exceeds those which have grown to the surface of the ground. A section through the base shows a single axial bundle which is connected with the bundle of the rhizome close to the base of a leaf. The stem of the stolon remains for a long time slender, and the narrow scale-leaves, which show no division into stalk and blade are remote from each other, being separated by about one-third of the circumference of the stem, but owing to the fact that the stem is somewhat twisted, it is not easy to determine whether or not the fourth leaf stands directly above the first. When quite small, the stolons are crowded between the base of the leaf and the rhizome, so that they are flattened, and the angle of divergence of the earliest leaves appears to be one-half. The surface, both of the stem and scale-leaves, is smooth and of a dark, reddish brown color. At the tip, the younger parts are greenish, chlorophyll apparently being formed, even when the stolon is completely underground, and of course shut off from the influence of light.

The stolon, when first formed, is very slender, but a short distance above its insertion it suddenly enlarges, so that it assumes a club-shape. Up to this point no leaves have been developed, and a section through the enlarged apex shows that this enlargement is due in part to the formation of the first leaves. The apex is nearly flat and much broadened on account of the increased lateral growth. It consists of a mass of small cells developed from the apical cell, and these soon become separated into plerome and periblem, the dermatogen not being readily made out in the very young stolon. The plerome in the basal parts is a simple cylinder of uniform size, but just below the first leaves, it widens suddenly, and divides later into two masses of procambium cells, separated by a mass of shorter ones. This division of the plerome cylinder takes place about the time that the first tracheary tissue is formed in the lower part of the stolon. As the permanent tissues develop in the bundle, this central mass of short cells forms the medullary parenchyma which communicates with the cortical parenchyma, by the foliar gaps, as in the main rhizome. The separation of the medullary parenchyma from the procambium begins before the bundle divides, thus occupying the center of the perfectly cylindrical bundle, and surrounded by an uninterrupted mass of procambium, which ultimately forms the hollow axial bundle that traverses the stolon for a short distance from its base.

The apex of the older stolons is more conical, and the apical cell has the form of that of the mature stem: — a tetrahedron with nearly equal lateral faces from which segments are cut off in the same way. The mass of meristem cells developed from them can soon be separated, as in the younger stolon, into plerome and periblem, the former soon showing the central shorter cells and the outer elongated procambium cells, the procambium cylinder being interrupted by masses of shorter cells like those of the medulla, and connecting the latter with the cell of the periblem. These spaces, the foliar gaps, become later much elongated on account of the great length of the internodes, but there are but three of them in a single cycle, corresponding to the primitive one-third arrangement of the leaves like that of the young germ plant, each leaf probably representing a segment of the apical cell.

The first tissue to assume the permanent form is the cortical parenchyma which in the slow-growing younger stolons can be traced up nearly to the apex. The cells are irregularly polyhedral in form, and distinct pits are early developed upon their walls. They contain small starch grains in considerable quantities, but no other conspicuous contents. No definite hypoderm is formed in the young stolons, but one or two layers of the outer cells acquire, very early, dark brown walls. The ground tissue is almost complete and its cells full grown, before any permanent tissue is developed in the fibro-vascular bundle. The procambium cells are long and narrow with oblique ends, and filled with granular, but colorless protoplasm. The first to be transformed into permanent tissue are situated nearly in the center of the axial bundle in the base of the stolon. A number of the cells of the procambium develop narrow transverse pits upon their walls, thus forming a mass of short scalariform tracheids, from which the formation of tracheary tissue proceeds, following lines nearly parallel with the circumference of the bundle. Sometimes a complete circle is formed, sometimes they extend hardly more than half-way round. The secondary tracheids are broader, but not very long, and often with the lateral walls somewhat sinuous. Their walls develop perfect scalariform markings.

In the two bundles found higher up, formed by the division of the plerome cylinder into two unequal parts, much the same process takes place, the tracheary tissue beginning with small scalariform tracheids near the center of the bundle, or sometimes toward one side, and the subsequent ones are formed within, and also towards the sides.

In the earlier formed parts of the stolon the bundle undergoes little further change except that a sheath is formed about it, and it is difficult to say whether some of the cells represent the parenchyma or sieve-tissue of the more perfect bundle of the main stem.

Just before the stolon appears above ground, the internodes become very much shorter and the leaves, instead of being scale-like, assume the character of foliage leaves. The young leaves are crowded together so that the end of the stolon is much thicker than its subterranean portions. In the cases observed, there were usually two fronds developed above ground almost simultaneously, differing so much in appearance from the later ones that, were their origin unknown, they would not be recognized as belonging to the same species as the mature fronds. Their pinnae are much fewer, and less crowded; the lobes less deeply cut, and their margins somewhat crenate; the whole frond looking much like the earlier ones of the germ-plant. Sometimes these appear to be the only leaves developed the first season, but in others later ones were formed, which, though small, had all the characteristics of the perfect leaf. The plant is now, in everything but size, complete, and soon becomes severed from the parent plant by the decay of the base of the stolon, thus becoming independent.

In one case a young branch was observed upon a stolon that had recently appeared above ground; this appeared to be developed, not as an adventitious bud, as in the case of the stolons themselves, but in the same way as a leaf, seeming to have taken the place of one of them. Its fibro-vascular bundle was continuous with that of the stem, which was still undeveloped, none of the permanent tissues having yet appeared. The end of this branch had developed the rudiments of two leaves and was in all respects like the end of any stem. Both stem and leaves had already developed scales.

Section VI. The Root.

The roots are produced in abundance from and near the bases of the older leaf-stalks. Each primary root develops numerous secondary ones that are arranged in two ranks in opposite sides of the main one. In all but the youngest parts the root is covered with a sort of dark brown cortex, formed by the remains of the epidermis and the underlying cells.

The development of the main roots can best be seen on the earlier aërial leaves of a stolon, as it is less difficult to make satisfactory sections than in the thicker mature stems. They arise from the bundle-sheath of the stem-bundle before any permanent tissue is developed, a short distance below the insertion of the leaf. Later ones arise from the broad bases of the stipe, and such have their bundles connected with one of the leaf-bundles. The primary roots grow rapidly, soon breaking through the overlying tissue; this taking place about the time that the tracheary tissue begins to form in the bundle with which they are connected.

The growth of the root from the apical cell is best studied in roots from an actively growing plant, that is, in spring or early summer. Such roots are light colored at their growing points, and their longitudinal sections through the tip will usually show very satisfactorily the formation of the tissues. As seen from the side, the apical cell (Pl. 7, fig. 6, *a*) is nearly triangular in outline, and in large roots is of very large size and easily seen. In smaller ones, where growth is slow, it is smaller and not so readily detected, although its form is often more regular, as in actively growing roots, the growth of the younger segments cut off from it often causes the sides to be bent (fig. 6). The outer wall, which is usually broader than the lateral ones, is slightly convex. If a series of transverse sections is made near the end of the root, one of them may pass through the apical cell, which viewed from above appears also triangular (fig. 7), but the sides are unequal. This shows that the cell, like the apical cell of the stem, is tetrahedral in form, the base being directed toward the apex of the root. The apical cell contains a large globular nucleus and the protoplasm is granular but not sufficiently so to render the cell opaque, in which respect less difficulty is experienced than in the other parts of the plant.

The succession of the segments is very regular and can be traced with comparatively little trouble. Each series consists of four cells, three from the lateral faces, which give rise to the tissues of the root itself, and one from the outer face, the cap-cell, from which the cells of the root-cap are formed. Each segment is at first a tabular cell, with the broad faces triangular. In order to see the first division in each of the segments, transverse sections through the young segments are necessary (Pl. 7, fig. 7). If this is done it will be found that each segment is first divided into two cells by a radial wall (sextant wall). The sextant wall does not divide the segment into quite equal parts, as its inner edge is in contact with one of the lateral walls of the segment some distance above its inner angle (fig. 8). Each of the two parts of the segment is next divided by a tangential wall into two cells, an inner and an outer one (fig. 6). From the series of inner cells the central fibro-vascular bundle is derived; from the outer, the ground tissue and cortex, each outer cell of the segment dividing into two by a second tangential wall, from the outer of which the cortex is formed, from the inner the ground-tissue. Almost simultaneously with these divisions, others are formed parallel to the sextant walls, but for some time no walls are formed parallel to the wall by which the segment was cut off from the apical cell, and consequently each segment remains in the form of a single layer of cells, until about two full rows of segments have been cut off. As a result of the divisions of the segments being thus formed, the depth of the segments increases but little as compared with the lateral growth, and the end of the root is nearly flat.

The mass of meristem arising from the division of the segments, becomes very soon differentiated into three concentric masses. The central one of plerome is cylindrical forming ultimately the fibro-vascular bundle, and, as before stated, arises from the inner cells of the segments. Its cells become rapidly transformed, by longitudinal walls, into a mass of narrow cells, the procambium (Pl. 7, fig. 6, *z*). Lying immediately around the plerome cylinder is a layer several cells in thickness, whose cells are broader than those of the plerome and which can be traced back to the inner of the two cells, formed by the second division of the semi-segments. This is the periblem (fig. 6, *y*) giving rise to a ground tissue. Outside is the third layer, or dermatogen, arising from the outer cells of the segments and forming the epidermis and cortical parenchyma, or such hypoderma as may be present. The limits of these three primary tissue-masses can be traced back to the youngest segments, as there is little displacement of the original cell walls through subsequent growth, this being also true in cross-sections (fig. 8), the sextant walls being perceptible in sections made some distance from the apex, and in such sections the successive divisions of the plerome cells can best be studied. Each of the original plerome cells is first divided by a tangential wall into an inner and an outer cell, the latter being again quickly divided by a radial wall. The inner cell seems to have the same process repeated again, but beyond this the divisions do not appear to follow any regular order. In the periblem, no definite order could be detected in regard to the formation of the division walls, but in the dermatogen cells of the seventh or eighth segment from the apical cell walls are formed almost simultaneously, at right angles to the longer axis of the cells, so that the segment, seen from the surface, shows a double row of cells of nearly equal size. As a result of this division, the cells of the dermatogen are shorter than those of either plerome or periblem.

All of the meristem cells have large nuclei and granular, but almost perfectly colorless, contents, and usually sufficiently transparent to make their study an easy matter.

The first division in the cap-cell is nearly parallel to one of its lateral walls, and the cell seen from above appears divided into two cells, one of which is triangular, the other quadrilateral. The segment soon loses its triangular form, becoming nearly circular and a second wall is formed perpendicular to the first, thus dividing the segment into four nearly equal cells, arranged like the quadrants of a circle. These subsequently become further divided by both radial and tangential walls, but not by walls parallel to the outer wall of the apical cell, so that they retain permanently the condition of single layers of cells.

The wall by which the cap-cell is first separated from the apical cell is not perfectly parallel to the outer wall, but is somewhat flatter, so that seen at first the segments are somewhat higher in the middle than at the sides. As it develops, the cells in the center elongate more rapidly than those at the sides so that this inequality becomes more and more marked as the segments become older, and the tip of the root finally becomes decidedly conical, although the end of the root itself is nearly flat.

In the rapidly growing root, only the outer cells of the root-cap are brown, but in the more slowly growing ones, all but those near the apical cell have their walls somewhat thickened and brown, and the cell-contents dried up.

The differentiation of the parts of the fibro-vascular bundle from the plerome does not begin until that of the ground tissue, hypoderma and epidermis is far advanced. At this time, the plerome consists of a mass of narrow procambium cells, those toward the circumference being somewhat shorter and with less oblique ends; those of the central ones being generally strongly oblique, so that the cells derived from them have sharply pointed ends, fitting closely together with no intercellular spaces. The cells increase greatly both in length and breadth, reaching nearly their full size before they begin to show any differentiation. The cells are filled with colorless protoplasm, almost destitute of granules, and with a large and distinct nucleus, especially in the outer ones. The procambium cylinder is broader in one direction, so that the section is elliptical. The first permanent tissue is formed near the foci of the elliptical bundle, there being formed almost simultaneously at both foci a single row of narrow, spiral tracheids. These are long with pointed ends, fitting closely together. At first the spiral markings are very fine and close, but with further growth they separate somewhat and also become thicker. A long row of them is completed before any trace of other tracheary tissue is to be found. Around these primary tracheids are next formed two or three rows of similar ones, and from the formation of tracheary tissue proceeds toward the center of the bundle.

An examination of the tissues of the complete root show that the tissues are less fully developed than in the aërial parts of the plant or the rhizome. The outer cells are dry and broken, and from them are seen growing the remains of numerous root-hairs, which, except in the younger parts, are also dry and brown.

The lateral roots arise in strictly acropetal succession and are arranged in two rows on opposite sides of the larger roots. Their formation begins before the tissues of the bundle of the main root are differentiated. Just before the primary tracheids are formed in the latter, the apical cell of the secondary root is formed from one of the cells of the bundle-sheath. The exact method of the formation of the apical cell was not traced, but it seemed to arise from the formation of three walls in one of the cells of the bundle-sheath so placed, as to include, together with the outer wall of the cell, a tetrahedral cell. This at once begins to grow and divide in the same way as the apical cell of the main root, and the young root breaks through the overlying tissues of the main root about the time that the first scalariform tracheids of the latter are complete. Its tissues develop in the same way as those of the main root, and the tracheids in the lower part are in direct contact with its primary tracheids. The major axis of the bundle of the secondary root is at right angles to that of the main root.

The bundles of the secondary are joined to that of the main root, the secondary root being at right angles to the latter, a line passing through the center of the bundle being coincident with the plane traversing the major axis of the main bundle. The bundle-sheaths are continuous and the tracheary tissue of the base of the secondary root ends abruptly against that of the main root, the tracheids of the former being smaller than the adjacent ones of the main root, and bent and flattened at the points of contact. Owing to the distortion of these basal tracheids, the bundle is larger at the base than elsewhere. The other elements of the bundle are also bent so as to connect the corresponding parts of the two bundles. The structure of the lateral roots is essentially the same as that of the main root, but the section of the bundle is more nearly circular.

Section VII. The Sporangium.

The development of the sporangium begins while the fertile frond is still small, and in order to procure the youngest stages most satisfactorily, it is necessary to begin with them when the fronds are just beginning to unroll. The margins of the pinnae are so strongly revolute (Pl. 7, fig. 10), that the whole lower surface of the lobes is completely covered, the margins acting as an indusium.

The young sorus (fig. 11) arises as a small prominence above a young vein, and is formed by a rapid growth of cells at and just below the surface. This prominence soon becomes hemispherical, and the formation of the sporangia begins. These arise as papillae from the superficial cells of the receptacle and are, therefore, morphologically, trichomes.

All the cells of the young receptacle are colorless, filled with fine granular protoplasm, and distinctly nucleated. The cell from which the sporangium is to arise (fig. 13, *m*) soon becomes slightly convex, dividing then by a wall parallel to the surface into two cells, an outer and an inner, the former (fig. 14) being the mother-cell of sporangium, the other taking no further part in the formation of the sporangium. Sometimes, but not usually, the original cell appears to undergo a preliminary division before the mother-cell of the sporangium is cut off. The mother-cell rapidly enlarges, assuming first a hemispherical form, and then elongating so as to become rather pear-shaped. After reaching this stage it is divided by a wall parallel to that by which the mother-cell was formed, into two cells, the lower of which forms the pedicel, the upper the capsule of the sporangium (fig. 15). In the earlier sporangia the upper cell undergoes several divisions before any more are formed in the lower one, but in those formed later, the pedicel lengthens rapidly in order to bring the young sporangium on a level with those previously formed, and it undergoes several divisions very early, so that on examining an older sorus, it is not at all uncommon to find very young sporangia in which the pedicel is many times longer than would be the case in those of the same age taken from one of the younger sori.

The first division in the capsule is nearly vertical, but usually slightly inclined, so that the resulting cells are not quite of equal size (fig. 16). Following this is a second wall inclined to the first at an angle of about 60°, and next a third, parallel to the outer wall of the capsule, and meeting both of those already formed (figs. 16-19). If a sporangium is now examined from above (fig. 19), it will be seen that both edges of the first wall are in contact with the outer wall of the capsule; that the second has one edge in contact with the first wall, and one with the outer wall of the capsule; while the third, which is nearly triangular in form, touches the wall of the capsule with its upper edge only, the other two being in contact respectively with the first and second. Finally a fourth wall is formed parallel to the upper surface of the capsule, but not touching its outer wall at any point, its three edges being in contact with the three walls just described (figs. 18–20). The capsule now consists of five cells, four parietal ones, tabular in form, and a central tetrahedral one, the *archesporium*. By the time that the capsule has reached this stage, the pedicel has usually undergone division by a longitudinal wall, into two unequal cells (fig. 20). The larger of these divides again by a second longitudinal wall, and the three cells thus formed become divided by a series of transverse walls, so that the pedicel when complete consists of three rows of cells. These are short at first, except in the later formed sporangia, but finally become about four times as long as broad (figs. 24, 26).

The archesporium now becomes divided by walls parallel to the first walls formed in it, and developed in the same order (fig. 21). These are the primary tapetal cells, and, while they are forming, the parietal cells undergo further divisions by walls perpendicular to the surface of the capsule, but directed in various directions (fig. 21). Walls are never formed in the parietal cells parallel to the surface of the capsule, so that the wall of the complete sporangium is a single layer of cells.

The tapetal cells very soon become also divided by walls perpendicular to their broader faces (figs. 21, 22), so that at this stage the central cell of the archesporium is surrounded by a double layer of cells. Somewhat later, about the time that the central cell becomes divided for the second time, the tapetal cells become further divided by walls parallel to the outer walls of the central cell, so that the tapetum is now composed of two layers of cells (fig. 23). These walls are not always perfectly parallel to the outer wall of the capsule, but frequently inclined more or less.

While these changes have been taking place, the sporangium has increased greatly in size, and become somewhat flattened laterally, this being much more strongly marked in the later ones which often do not fully develop.

A surface view of the young sporangium shows that the arrangement of the parietal cells is not the same in all parts. A row of cells running around the longest arc of the capsule has divided more rapidly by transverse walls than any of the other cells, resulting in the formation of a row of transversely elongated cells running all round the capsule (figs. 22, 24). As the sporangium increases in size these continue to divide in the same way until there are between thirty and forty of them. These are the cells of the annulus. The other parietal cells divide more slowly and by longitudinal as well as by transverse walls.

About the time that the annulus can first be distinguished, and just before the tapetum becomes two-layered, the inner cell of the archesporium begins to divide to form the spore mother-cells. The direction in which the first division takes place is not always the same, being in some cases nearly vertical, in others horizontal, but in either case more or less inclined (fig. 22). Following this a second wall is formed, nearly at right angles to the first, thus dividing each of the cells already formed into two (fig. 23). Almost simultaneously the two layers of the tapetum are completed.

The central cells, almost from the first, are distinguished from the outer cells by their more dense and highly refractive contents. They now undergo further division until the complete number, twelve, of the spore mother-cells is attained. The latter are colorless, but contain numerous fine granules, and each has a large and pretty evident nucleus. As soon as the full number is complete, the walls of the tapetal cells are absorbed and the mass of mother-cells, which are still connected, floats freely in the cavity of the sporangium which it does not nearly fill (fig. 24). The annulus has acquired nearly its full number of cells, and the whole sporangium its complete form, though still considerably smaller than when mature.

The spore mother-cells now become separate by the partial dissolution of their walls, and becoming rounded off float about in the cavity of the sporangium which they nearly fill, having increased very considerably in size after separating. Each spore mother-cell is at this stage globular, with a large, but not usually very distinct nucleus which is sometimes central in position, sometimes eccentrically placed. The protoplasm is somewhat less granular than before, areas of considerable size being frequently quite free from granules.

The first trace of division in the mother-cells is a change in the nucleus. This becomes larger and elongated and coarsely granular in appearance. In some cases observed at this stage, the nucleus was extraordinarily distinct. The nucleus increases greatly in size, but becomes much less distinct (fig. 25), and careful observation shows the formation of the nuclear spindle, but no satisfactory view of the nuclear disc could be obtained, although usually there was an evident line separating the two parts of the mother-cell, which at this stage has increased slightly in size and become somewhat oval in form. The two secondary nuclei are formed at the poles of the nuclear spindle and become, when complete, much like the primary nucleus. They very soon divide again, probably in the same way as the primary nucleus, resulting in the four nuclei of the young spores. Although there is a dividing line between the two masses of protoplasm into which the mother-cell first divides, no cell wall seems to be formed; but after the second division is complete, the young spores become separated by walls. The planes of division of the nuclei are at right angles, so that of the four resulting spores, two lie in one plane and two in another. After division is completed, the spores begin to lose the granular appearance they hitherto exhibited and become more transparent. They now separate, but remain sufficiently united to show which belong together and have become almost destitute of granular contents. They are kidney-shaped, slightly flattened on one side, but appear oval if seen from above. Each is provided with a very distinct nucleus, embedded in the protoplasm near the wall on the flattened side. The spores rapidly increase in size until they are about twice as large as when first formed, this increase being probably due to the using up of the material derived from the tapetal cells. Each spore has a distinct wall which is early partially differentiated into an inner and outer wall. A third coat, brown in color (the exospore), finally appears and attains considerable thickness. It becomes provided with a series of ridges or folds (fig. 27), but even when young is easily separated from the spore by slight friction. Before the exospore is formed, very fine granules are seen to appear, most abundantly in the vicinity of the nucleus. These rapidly enlarge and are seen to undergo division. About the time that the exospore begins to develop, some of them become tinged with chlorophyll, and continuing to form rapidly, the spore soon becomes densely crowded with them, so as almost to conceal the nucleus and render the whole spore almost perfectly opaque and dark green. The nucleus changes its position, moving toward the center of the spore, the exospore reaches its full thickness, and the spore is complete.

While the spores have been developing, during which time they have grown so as to fill the sporangium completely, the parietal cells of the sporangium have also undergone marked changes. The cells of the annulus, which at first were distinguished from the other cells simply by their form, begin to project above the level of the others and their division walls become thicker. At this stage (fig. 24) all the parietal cells are transparent and colorless, and are distinctly nucleated. The cells of the annulus on one side of the sporangium are rather more elongated transversely than the others, these being very much more strongly marked in four, or sometimes only three, near the base of the capsule, forming the *stomium*, or point at which the capsule opens. The division walls are also thicker in the cells of this structure which is specially well developed in the fern under consideration.

About the time that the spores are fully grown, but before the exospore is completed, the walls of the parietal cells begin to assume a brown tinge, this beginning with the cells of the annulus, whose division walls show it first. The color is at first pale yellowish, but the walls darken rapidly, until when mature they are a dark, almost perfectly opaque brown. The contents of the parietal cells disappear, leaving them dry and brittle, and when ripe, by the contraction of the cells of the annulus, the capsule is burst, the opening taking place at the stomium and the spores are discharged.

Each sorus develops a small indusium (fig. 12, *in*), which is nearly semicircular and attached by its lower margin to the base of the receptacle, separating the sori. It never attains much size and early withers away, its place being taken by the revolute margin of the leaf, this being thin and membranaceous, consisting for nearly half its width of a single layer of cells, which finally become dry and scarious, completely covering the sori (figs. 10, 28).

There are five sori developed upon each pinna-lobe of the fertile frond. They are at first sessile (fig. 11), but soon are elevated upon a pedicel, from whose central cells a short fibro-vascular bundle is formed connected with the vein above which the sorus arises (fig. 12). When complete they are so large that they touch one another, so that the whole lower surface of the leaf appears to be covered with sporangia.

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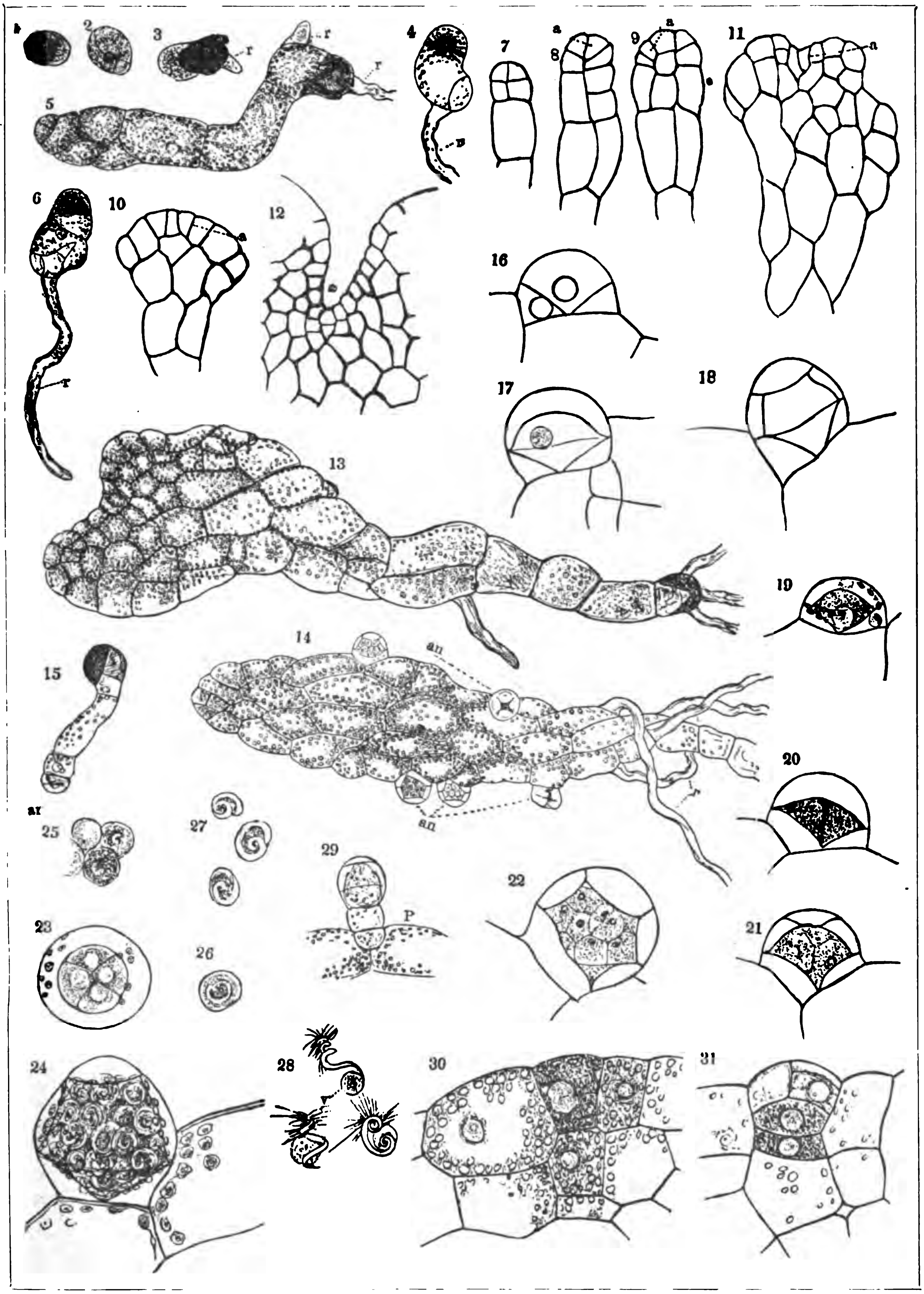

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